

# The soil fauna

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*Earthworms, though in appearance a small and despicable link in the chain of nature, yet, if lost, would make a lamentable chasm...worms seem to be the great promoters of vegetation, which would proceed but lamely without them—Gilbert White of Selborne.*

Members of the soil fauna (animals) are ascribed all manner of attributes, from plant pests to predators to soil enhancers. In this chapter, we describe both **invertebrate** animals that live in the soil and their habitat and additionally examine their activities in the context of the soil food-web (Fig. 8.1). We focus on the role of soil animals in controlling microbial pathogens, mineralizing nutrients, changing microbial community composition, and enhancing primary production. Like aboveground fauna, the physical structure of the ecosystem places constraints on the activities of the soil fauna, especially in relation to the microflora. Because of these constraints, the activities and interactions of the soil fauna are also discussed in the context of the soil physical environment. Climate change—through its effects on soil moisture and temperature dynamics—also impacts faunal activities and interactions and is addressed throughout the chapter.

The organisms that use the soil as habitat at some point in their life are numerous and span all three domains of life on Earth. As with archaea, bacteria, fungi, cyanobacteria, and viruses, only a fraction of the soil fauna has been described. For example, only about 4000 earthworm species have been described of the estimated 8000 species on Earth. For our purposes, the soil fauna includes those animals that spend a significant portion of their life cycle within the soil profile or at the soil–litter interface. In this chapter, we will focus on the **earthworms**, **microarthropods** (mites and collembolans), **nematodes**, and **protozoa**. Phylogenetically, organisms in the first three groups belong in the kingdom Animalia, whereas protozoa belong in the kingdom Protozoa.

Despite the obvious morphological differences among them, soil animals share a number of similarities:

- They are **eukaryotes** (Chapter 1).
- With few exceptions, they are **aerobes** and use oxygen as a terminal electron acceptor. The exceptions are some species of nematodes and protozoa that are **facultative anaerobes** (i.e., they can tolerate anoxic conditions but use oxygen preferentially).

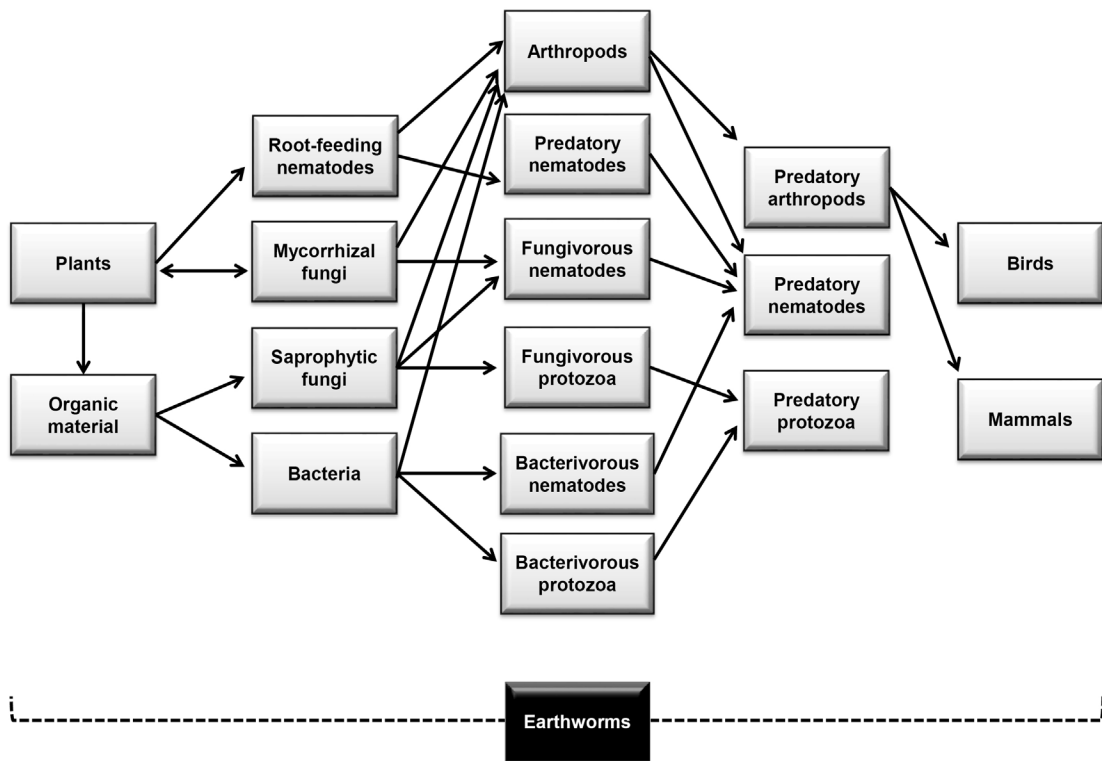


FIGURE 8.1 The soil foodweb showing multiple interactions among plants, soil fauna, and soil microorganisms. Earthworms interact with various groups of organisms within the foodweb.

- They are **chemoheterotrophs** because they meet their carbon and energy needs by metabolizing organic compounds (Chapter 3).
- They are **motile** and travel distances proportional to their size by propelling themselves on their own power. Generally, earthworms travel meters, collembolans (springtails) centimeters, and nematodes and protozoa a few millimeters.

## Habitat

Soil animals differ in the ways that they inhabit the soil, partly dictated by differences in their size. The length and width of an organism constrains its ability to take advantage of habitat and food resources. The soil fauna can be divided into three size groups, based on their body width: (1) **macrofauna** (>2 mm), represented by earthworms; (2) **mesofauna** (0.1–2 mm), represented by mites, collembolans, and nematodes; and (3) **microfauna** (<0.1 mm), represented by protozoa (Fig. 8.2). The soil faunal community is also divided into organisms that are essentially **aquatic** (living in water-filled pores; e.g., protozoa and nematodes), organisms that are **aerial** (living in the air-filled spaces; e.g., microarthropods), and

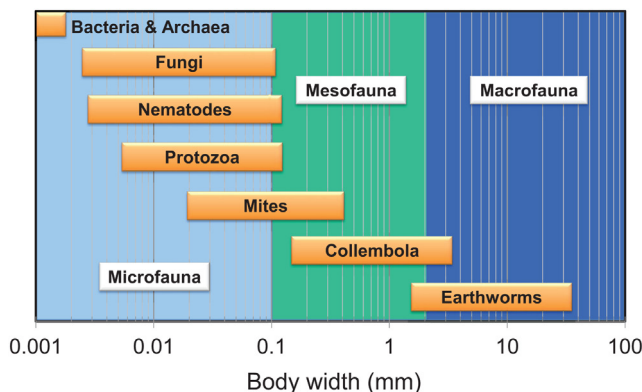


FIGURE 8.2 Body width ranges for soil organisms.

those that engineer their own space (e.g., earthworms; [Heal and Dighton, 1985](#)). As noted in [Chapter 2](#), soils comprise three states of matter: solid, liquid, and gaseous. From an ecological perspective, this is a good description of the partitioning of habitat available to soil organisms (see [Fig. 1.1](#)) that are not engineers. Soil pore spaces vary in size, water content, and air, resulting in variations in habitat:

- Members of the microfauna are generally sufficiently small to fit into **mesopores**, which are 30–100  $\mu\text{m}$  in diameter, and **micropores**, which have diameters less than 30  $\mu\text{m}$ . These pores are found within soil **aggregates** (or **peds**) and retain water at matric potentials less than field capacity ( $< -0.03$  MPa). Thus, the basic unit of habitat for aquatic organisms like nematodes and protozoa is the water-filled pores of aggregates ([Hattori, 1994](#)). Relatively small aggregates (5 mm in diameter) can be home to hundreds of protozoa and tens of nematodes.
- Members of the mesofauna fit within pores with a diameter larger than 100  $\mu\text{m}$  (**macropores**), especially the spaces between aggregates. Interaggregate pores drain quickly, making good habitat for these generally aerial organisms.
- Members of the macrofauna do not fit within the existing pore structure of soil, so they either create their own habitat by burrowing into the soil, use burrows created by other organisms, or live on the soil surface.

The activities of burrowing fauna, such as earthworms, alter the soil habitat for many other types of organisms by changing its physical structure and the distribution of resources. Burrows increase aeration and water movement within the soil profile. Greater gas exchange between the soil and the atmosphere increases the availability of oxygen for aerobic soil microorganisms and plant roots. Earthworm casts and soil lining earthworm burrows (the so-called “**drilosphere**”) have a different porosity from bulk soil. The smaller pores created in the burrow walls may provide more habitat for nematodes ([Görres and Amador, 2010](#)).

A given pore space may be filled with water or air, depending on the current soil water potential. When soil dries, the habitat of the aerial soil community expands, and shrinks when soil becomes wet. The reverse is true for the aquatic soil fauna. These changes in water-filled pore space take place in response to rainfall, irrigation, snowmelt, and evapotranspiration. By

altering the magnitude, intensity, and frequency of precipitation events and/or evapotranspiration, climate change can impact the habitat of both aerial and aquatic soil organisms. Thus, the availability of habitat for different kinds of animals depends on water dynamics as well as soil structure and texture, which control the distribution of pore sizes in the soil. This in turn affects decomposition/C mineralization rates, which are partially determined by soil matrix potential (Davidson et al., 1998).

Soil animals have a number of adaptations to survive environmental changes in the soil. For example, some mites—which are aerial organisms—survive flooding of their habitat by clustering together. The air bubbles trapped between their bodies satisfy their demand for oxygen when soil is saturated. Other aerial organisms, like collembolans, avoid saturated conditions by migrating. Some aquatic species, such as nematodes and protozoa, form **cysts**—life stages with thick membranes or walls—or enter a state called **anhydrobiosis** when soil dries. The latter is a strategy to survive desiccation as well as freezing temperatures that is characterized by an almost complete loss of moisture from the organism.

In addition to controlling habitat availability and suitability for soil organisms, the pore and aggregate structure of soil, in conjunction with soil moisture, controls the ecological interactions among soil fauna within the soil foodweb (Fig. 8.1). For example, as soil dries bacterivorous nematodes that prey on bacteria can become trapped in pores with their bacterial prey, increasing predation as well as excretion of mineral N by the predators (Savin et al., 2001). In contrast, increased soil wetting can increase movement of organisms between soil aggregates, allowing them to move more freely among aggregates to quest for food resources, as is the case with some protozoans and nematodes (Görres et al., 1999).

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## Functional groups of soil fauna

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### Earthworms

**Earthworms** (Animalia: Annelida: oligochaetes) exhibit external and internal segmentation of the body. They share this characteristic with other annelids including polychaetes, or bristle worms, found mostly in aquatic sediments, and leeches, as well as enchytraeids, also known as potworms—small, unpigmented soil worms.

Earthworms are either **hermaphroditic** or **parthenogenic**; although most species reproduce by cross-fertilization, parthenogenic species reproduce without sex, producing clones. Ova are contained in cocoons that are deposited at or near the soil surface. Adult earthworms range from a few centimeters to almost 2 m in length for several giant earthworm species and from 2 to 20 mm in diameter. Most earthworms mature within 2 years of emerging from the cocoon, although there are exceptions. For example, earthworms used for composting have much shorter maturation periods, because high fecundity is desirable in vermicomposting beds to replace worms removed with compost. Typical cocoon production varies among species but ranges from 0.1 to 2 cocoons per adult per day for *Lumbricus rubellus*, a temperate species, and *Perionyx excavatus*, a tropical worm and popular vermicomposting species, respectively. Cocoons may contain between 1 and 4 ova (Dominguez, 2004).

Earthworms are found in most ecosystems throughout the world except for deserts, areas with permafrost, areas without soil or vegetation, and mountain ranges. Based on current

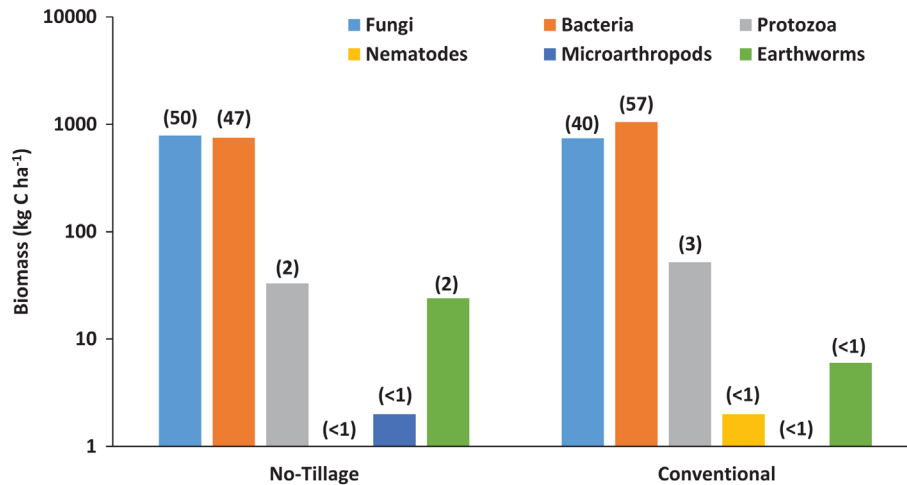


FIGURE 8.3 Relative biomass of microbial and faunal groups in conventional (CT) and no-tillage (NT) soils in summer/fall at Horseshoe Bend Experimental Area, Georgia, United States. Values in parentheses are percentage of total biomass. Source: Adapted from [Beare \(1997\)](#).

climate change predictions, their range is likely to expand into areas now covered in permafrost and contract in areas undergoing desertification. The number and species distribution vary considerably with the type of ecosystem, with numbers ranging from less than 10 m<sup>-2</sup> in agricultural fields to more than 700 m<sup>-2</sup> in forest soils. They are generally more abundant in undisturbed than disturbed environments. In agricultural ecosystems, their numbers depend on management practices employed. For example, earthworms constitute a greater proportion of the biomass in soil under no-tillage than under conventional tillage ([Fig. 8.3](#)).

To enumerate or identify earthworms, they must be driven out of the soil by drenching the soil with an irritant, such as a mustard or formaldehyde solution, or by saturating the soil with water. Electrical fields, vibration, hand sorting, and wet sieving are also used. As is true for other soil animals, estimates of the size and composition of earthworm communities are dependent on the method used ([Box 8.1](#)). The various methods introduce different biases into enumerations. For example, using mustard as a vermifuge was more effective for extracting anecic earthworms than applying an electrical field, while no difference was found for epigeic earthworms ([Eisenhauer et al., 2008](#)). When ecological experiments are conducted, the effect of a chosen method on non-target species needs to be considered ([Table 8.1](#)). For instance, chemical extraction methods may affect other species groups such as arbuscular mycorrhizae and other microorganisms. Destructive methods like hand sorting would preclude studying other species or processes in the same location where earthworms were enumerated.

Earthworms are classified into three ecological groups based on food source, pigmentation, adult size, burrow type, mobility, longevity, generation time, drought survival, predation, and other factors ([Bouché 1971, 1977](#)). These groups are:

- **Epigeic (upon the earth).** Worms in this group are small to medium in size (2–7 cm) and are heavily pigmented. They live at the soil–litter interface, do not form burrows, and

## BOX 8.1

**Extraction and enumeration—What are we counting?**

The **extraction efficiency** of methods used to count soil animals is invariably less than 100%. For example, extraction of nematodes from soil is at best 50% efficient. Furthermore, the efficiency may vary within a group of organisms. For example, one problem with extracting earthworms from soil with chemical irritants is that estimates of community composition may be skewed toward those groups that can get to the soil surface relatively quickly (anecic and epigeic), leading to undercounting of endogeic species. Different methods to count the same

organism may yield varying results because they rely on different attributes of the organism. The Baermann funnel (Fig. 8.7) method yields numbers of live nematodes because it requires that the nematodes swim out of the soil to be counted. By contrast, the sugar flotation method does not discriminate between dead and live nematodes. Finally, many soil animals have resting stages (e.g., nematodes can go into anhydrobiosis and protozoa form cysts) that allow them to survive unfavorable environmental conditions, and thus they may go undetected.

**TABLE 8.1** Efficacy of methods for the recovery of earthworms and their associated long-term side effects on non-target organisms in a temperate meadow soil.

| Methods                 | Earthworm extraction efficacy: |       |      | Non-target effects on: |          |           |             |            |             |
|-------------------------|--------------------------------|-------|------|------------------------|----------|-----------|-------------|------------|-------------|
|                         | Total                          | Adult | Juv. | Collembola             | Gamasida | Oribatida | G-<br>----- | G+<br>PFLA | AM<br>----- |
| <b>Chemical methods</b> |                                |       |      |                        |          |           |             |            |             |
| AITC [mmol]             |                                |       |      |                        |          |           |             |            |             |
| 0.5                     | +                              | ++    | +    | –                      | +        | –         | –           | –          | –           |
| 1.0                     | +                              | ++    | +    | –                      | –        | –         | –           | –          | –           |
| Formalin [%]            |                                |       |      |                        |          |           |             |            |             |
| 0.2                     | +                              | ++    | +    | –                      | –        | –         | +           | –          | +           |
| 0.4                     | +                              | ++    | +    | –                      | –        | –         | +           | +          | +           |
| <b>Physical methods</b> |                                |       |      |                        |          |           |             |            |             |
| Octet                   | ++                             | +     | ++   | –                      | –        | –         | –           | –          | –           |
| Handsorting             | ++                             | +++   | ++   | /                      | /        | /         | /           | /          | /           |
| Kempson                 | +++                            | +++   | +++  | /                      | /        | /         | /           | /          | /           |

AITC, allyl isothiocyanate; AM, arbuscular mycorrhizal fungi; G–, Gram-negative bacteria; G+, Gram-positive bacteria; PLFA, phospholipid fatty acids. Extraction efficacy: (+) = low; (++) = medium; (+++) = high. Nontarget effects: (–) = no negative long-term effects; (+) = negative long-term effects; (/) = destructive method, no possibility to observe non-target effects. Effects on bacteria and fungi were inferred from changes in the presence of their corresponding PLFAs.

Modified from Čoja *et al.* (2008).



**FIGURE 8.4** (A) Anecic earthworms make vertical burrows. Burrow opening is indicated by *white arrow*. The earthworms feed on litter from the surface, which they drag into the burrow. (B) Nightcrawler midden clearly raised above soil and assembled from leaf litter (*yellow circle*). (C) Same midden with leaf debris removed showing casting materials (*blue circles*) and a burrow lined with plant material (*yellow circle*). Source: Photo credit: (A) E. Nicosia, (B and C) Maryam Nouri Aiin.

ingest little or no soil. They eat decomposing litter or manure found on the soil surface. Birds, mammals, and arthropods prey heavily on epigeic worms. Red or blood worms (*Lumbricus rubellus*) are representative of this ecological grouping.

- **Anecic (out of the earth).** The common nightcrawler, *Lumbricus terrestris*, is an anecic earthworm. It makes permanent or semi-permanent vertical burrows that have an opening to the surface (Fig. 8.4). Anecic earthworms have some pigmentation and their adults are the largest of the three groups (typically 10–30 cm) if one excludes the various species of giant earthworms. They feed on decomposing litter on the soil surface, which they pull into their burrows, where further decomposition takes place. They deposit their **casts** (excreta) within their burrows and on the soil surface. A **midden** consisting of the casts along with organic debris is often found as a raised pile near the opening to burrows. Although burrows provide some protection, anecic earthworms are still subject to predation by birds at the soil surface and by moles.
- **Endogeic (in the earth).** These subsoil species are represented by the genus *Diplocardia*, the most abundant indigenous species in the southeastern United States. Other common species in this group belong to the genus *Aporrectodea*, which are exotic in North America. Endogeic earthworms make extensive horizontal or semi-horizontal, continuous burrows within a few centimeters of the soil surface. Endogeic worms generally lack pigmentation and are intermediate in size between anecic and epigeic earthworms. They feed on the organic matter fraction of mineral soils and therefore prefer those with high organic matter content. Because they reside within the soil profile, the predatory pressure is low.

Earthworm classification by ecological group can broadly be done by color. Pigmented worms tend to spend time at the surface whereas the unpigmented worms tend to be endogeic worms. This level of classification is at a very broad scale, and earthworm species that belong to one genus can be part of all three groups. *Lumbricus*, the genus to which the common night crawler belongs, is one such genus. From an ecological point of view, the community composition according to both species and ecological group is important. However, identifying species is often hampered by lack of easily identifiable taxonomic characteristics

## BOX 8.2

## Using DNA to identify soil fauna

Classifying and counting soil organisms in a soil sample requires that they be identified taxonomically and that we account for all individuals in the sample. Traditional morphological identification of fauna is a rare skill among ecologists, and the methods of extraction can be particularly ineffective. Conversely, more recently developed methods employing nucleic acid analyses avoid the need for morphological identification. This is based on the principle that a species has unique DNA sequences of taxonomic value. Once we establish which sequences are uniquely associated with a morphologically identified specimen, the presence of these sequences, or **barcodes**, in the DNA of an unknown specimen allows us to identify it by comparison to barcodes deposited in a database. Similarly, the presence of a barcode in a DNA extract from a soil sample indicates the presence of particular species of fauna.

Different regions of the genome may be used to identify fauna, including the 18S ribosomal RNA region, which is unique to eukaryotes, as well as genes coding for mitochondrial cytochrome oxidase and microsatellite DNA found interspersed throughout the genome. These regions exhibit sufficient

genetic variation to allow us to distinguish among species. The process involves either extracting DNA from a soil sample (for meso and microfauna) or from organisms isolated from a soil sample. The extracted DNA is mixed with primers targeting a particular region of the genome and the enzyme DNA polymerase. This process, known as the **polymerase chain reaction** (PCR), produces thousands of copies of a sequence, which can subsequently be used for quantification of the number of copies of the sequence (quantitative PCR). Alternatively, the PCR product can be sequenced using high-throughput technology (Chapter 4) and compared to a database of sequences for previously identified fauna.

This approach has been used successfully to identify novel species of earthworms (Boyer et al., 2011) and to assess soil faunal diversity (Horton et al., 2017). It has led, for example, to the discovery that the earthworm *Dendrodrilus rubidus*, which was regarded as an exotic species of European origin, may have originated in America. It is now called *Bimastos rubidus* (Csuzdi et al., 2017), re-assigned to a genus found in America based on genetic analysis.

and by the fact that there appear to be species that are sufficiently different to be distinguished genetically but not morphologically. For example, DNA sequencing (Box 8.2) has determined that the morphological species *L. terrestris* (night crawler) includes a cryptic look-a-like called *L. herculeus* (James et al., 2010).

Because earthworms cannot regulate their water content or body temperature, their activities are dependent on soil moisture and temperature. When adverse conditions occur, they migrate to areas of the soil profile compatible with their needs. For example, during dry, hot conditions, anecic earthworms migrate farther into the soil profile, seeking greater soil moisture and milder temperatures. They come back to the surface to feed at night when the soil has cooled. If hot and dry conditions persist for long periods of time, they will go into a

dormant state known as **aestivation**. When it is cold, they burrow below the frost line and remain dormant until the soil warms up sufficiently for them to resume their activities. The well-known phenomenon of earthworms emerging to the surface during a rainstorm may have several explanations. The most credible of these are: avoidance of predators which may cause vibrations in the soil similar to those set up by raindrop impact; ability to migrate further on the surface; and greater ability of hermaphrodites to more easily find a mate at the surface. The explanation that they avoid drowning in saturated soils is not convincing since rainwater contains sufficient dissolved oxygen.

At a much larger geographic scale, a group of earthworms known as **cosmopolitan worms** (Box 8.3) may be expanding their range at the northern boundary because of global climate change. For example, several earthworms in the megascolecid family originating in Japan appear to have extended their range from southern to northern New England over the past 30 years. This may have been due to the extension of the frost-free period during the last few decades, which has lengthened the growing season by 20 days. If this trend continues, Canada will be susceptible to a megascolecid invasion.

The effects of earthworms on the soil ecosystem depend to a large extent on the ecological group to which they belong, because this determines their level of interaction with soil and the organisms that live within the ecosystem. Thus, epigeic worms have little direct effect on what goes on in the soil because they live and feed at the soil–litter interface. Their main effects may be **comminution** (grinding) of litter or competing for plant detritus with other litter-feeding organisms, including anecic worms. By contrast, anecic worms can have a number of direct effects on the soil ecosystem, from creating habitat for microorganisms to causing shifts in the composition of microbial communities. They also repack organic matter into small micro-aggregates where it is protected from decomposition (Knowles et al., 2016), depriving microorganisms of access to substrates. This mechanism of carbon sequestration may have broader implications by helping to balance out increased greenhouse gas emissions (Lubbers et al. 2013; Zhang et al., 2013) associated with the activities of other types of earthworms.

## Microarthropods

Arthropods have segmented bodies, jointed legs, and a cuticle that acts as an exoskeleton. Insects, mites, and spiders are arthropods. The two most abundant groups of soil microarthropods are the **collembolans** (Animalia; Arthropoda, Insecta) and **mites** (Animalia, Chelicerata: Arachnida). They are found on or near the surface of the soil and in plant litter. Populations range between  $10^3 \text{ m}^{-2}$  in agricultural soils and  $10^6 \text{ m}^{-2}$  in forest soils.

Collembolans, also known as springtails, are wingless insects a few millimeters in length and 0.2–2 mm in width (Fig. 8.5). They get their common name from the ability of springtails that live above-ground to catapult considerable distances using their furcula, a tail-like, forked organ. However, this organ is reduced or not present in soil-dwelling collembolans, an adaptation to subterranean life. They are aerial organisms but are susceptible to dry as well as saturated soil conditions. They are sufficiently small to fit within interaggregate spaces in soil where water drains freely. They are thought to be **omnivorous**, feeding on bacteria, fungi, nematodes, algae, other collembolans, and decaying plant material. Ecologically, springtails that consume plant detritus are regarded as shredders that fragment the litter and increase

## BOX 8.3

## Exotic soil fauna

Conservation biology places importance on the dispersal of species to places beyond their original range. These introduced or exotic species can become a threat to native ecosystems when they become invasive. Plants and aboveground vertebrates are familiar examples of invasive organisms, which are often regarded as weeds or pests. Soil fauna can also be invasive—earthworms, ants, flatworms, and springtails are examples of soil organisms that have spread beyond their original range.

Earthworms can be invaders of soil ecosystems, particularly in areas where native species were extirpated during the last glaciation. In North America, earthworms from Europe (Lumbricidae) and Asia (Megascolecidae) have invaded the formerly glaciated areas of the northern tiers of the United States and southern Canada but can also be found south of the extent of the last glaciation. Their presence initially changes forest soil structure through the consumption of the thick folistic O-horizon that developed in the absence of earthworms. This sets off a cascade of events that may begin with the reduction of forest plant biodiversity, thereby depriving other decomposer species of resources and habitat and additionally affecting populations of potential predators, for example, salamanders, and of some ground-nesting bird species whose nest are deprived of vegetative cover and become vulnerable to

nest predators. Earthworms are dispersed by commercial plant material, composts, and fishing bait. Earthworm invasions are culturally cryptic because they are regarded as beneficial organisms in agriculture and gardening. Thus, they go undetected as invaders of forests.

Flatworms (or hammerhead worms) from Asia and New Zealand have been introduced to the United States and most of Europe. In parts of the United Kingdom, *Artiopsotia triangularata* (the New Zealand flatworm)—which was probably imported with ornamental plants—has decimated earthworm populations. The two most abundant flatworm species invading American ecosystems, *Bipalium adventitium* and *Bipalium kewense*, are widespread in New York and are found in several other states. Tetrodotoxin, the same neurotoxin found in pufferfish, is present in these flatworm species and is likely the substance that paralyzes their earthworm prey.

Unlike earthworms and flatworms, smaller exotic organisms such as springtails (Collembola) are likely to go unnoticed. For example, the table here shows that collembolans on the remote Macquarie Island, located between New Zealand and Antarctica, originated in Europe and North and South America. They likely entered the island with supplies (mainly plants) to the local research station around which these organisms are commonly found.

Exotic springtails (collembola) on remote sub-Antarctic Macquarie Island.

| Family          | Genus               | Species                  | Original locality   |
|-----------------|---------------------|--------------------------|---------------------|
| Entomobryodae   | <i>Lepidocyrtus</i> | <i>violaceus</i>         | France              |
| Hypogastruridae | <i>Hypogastrura</i> | <i>viatica</i>           | Scandinavia         |
| Isotomidae      | <i>Desoria</i>      | <i>tigrina</i>           | Switzerland         |
| Isotomidae      | <i>Isotomurus</i>   | <i>palustris</i>         | Europe              |
| Katiannidae     | <i>Sminthurinus</i> | <i>quadrifasciatus</i>   | North America       |
| Katiannidae     | <i>Sminthurinus</i> | <i>mime</i>              | South America       |
| Onychiuridae    | <i>Protaphorura</i> | <i>finata</i>            | Switzerland         |
| Sminthurididae  | <i>Sminthurides</i> | sp. cf. <i>malmgreni</i> | Northern Hemisphere |
| Tullbergiidae   | <i>Mesaphorura</i>  | <i>macrochaeta</i>       | Canada              |

Modified from [Convey et al. \(1999\)](#).

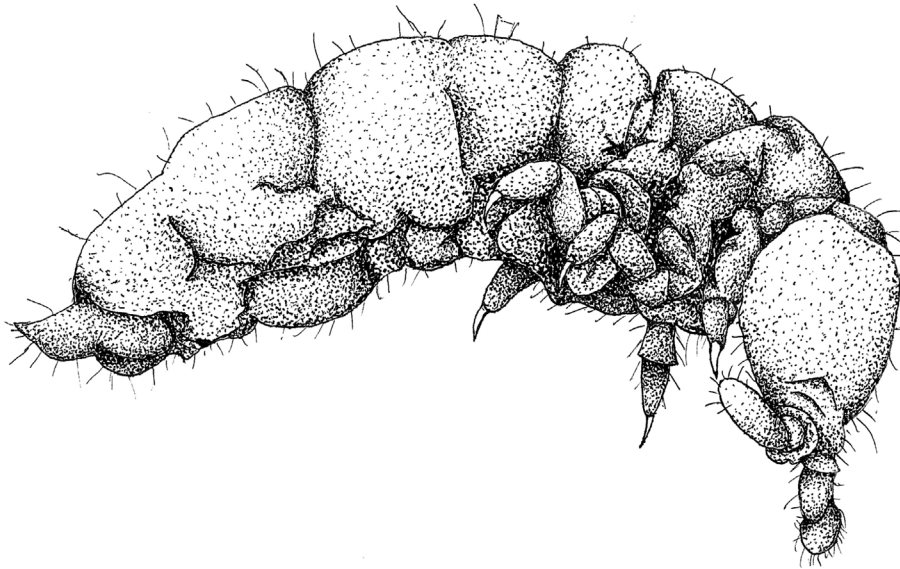


FIGURE 8.5 A soil collembolan (*Onychiurus* sp.). Collembolans that live within the soil tend to be more compact than those that live aboveground. Source: Drawing by Laura Amador, based on [Eisenbeis and Wichard \(1987\)](#).

the susceptibility of the litter to microbial colonization by increasing its surface-to-volume ratio.

Mites are the other important group of microarthropods in the soil ([Fig. 8.6](#)). They have oval bodies with four pairs of legs. Oribatid mites feed on fungi, decomposing plant detritus, or both. They tend to be the most abundant group of mites in many soils. The mesostigmatid mites are primarily predators of small arthropods and nematodes. Prostigmatid mites include some fungal feeders, but most species appear to be predators of small arthropods

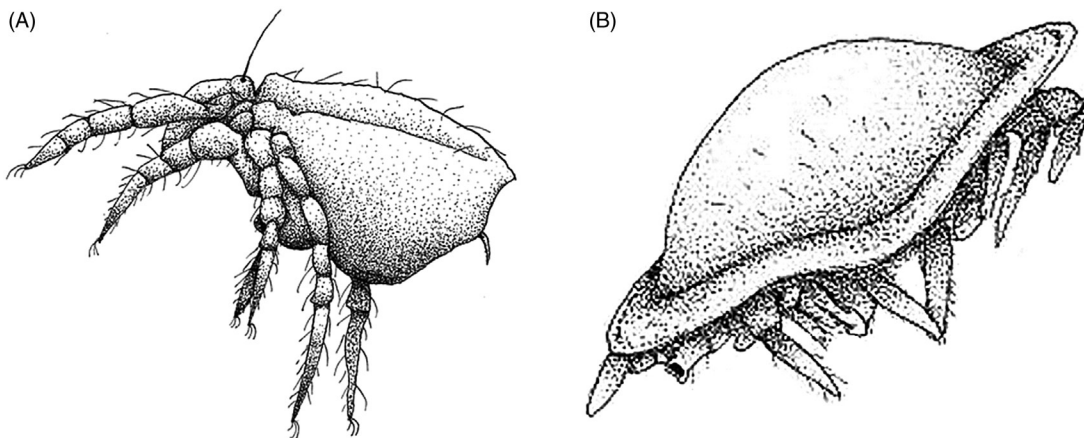


FIGURE 8.6 Examples of (A) oribatid (*Nothrus* sp.) and (B) mesostigmatid (*Uropoda cassidea*) soil mites. Source: Drawings by Laura Amador, based on [Eisenbeis and Wichard \(1987\)](#).

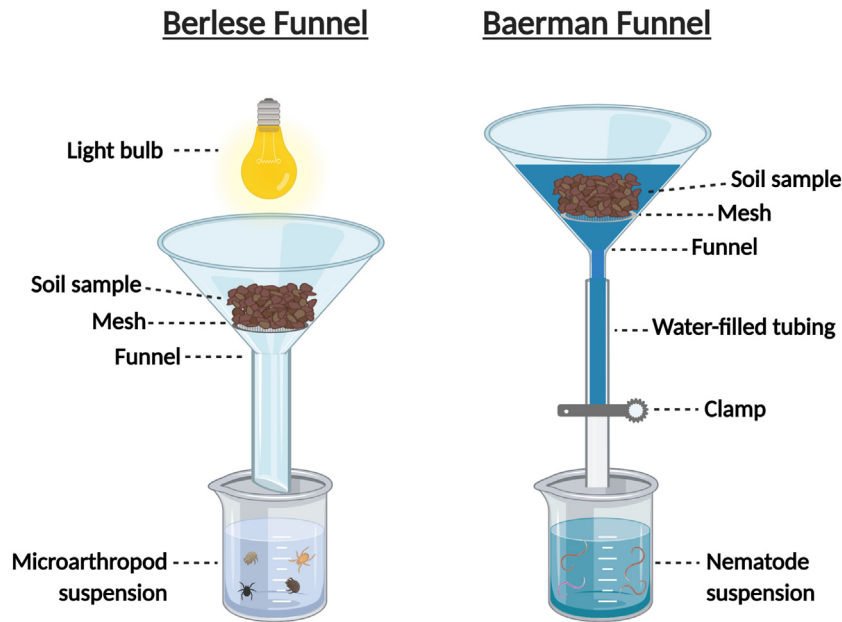


FIGURE 8.7 Schematic diagrams of a Berlese funnel, used to determine the number of microarthropods in soil, and a Baerman funnel, used to extract nematodes from soil. Source: Created with BioRender.com.

and nematodes. They can be distinguished from oribatid and mesostigmatid mites by the presence of a constriction between the anterior and posterior part of the body that is absent in the other two.

Determining the number of microarthropods in soil involves driving or floating them out of a soil sample (Moldenke, 1994). The *Berlese funnel* method involves placing the soil sample on a wire mesh within a funnel and applying an environmental stimulant (light, heat, or a chemical irritant) that forces the organisms out of the soil (Fig. 8.7). The mites fall through the mesh and are collected in a bottle placed below the funnel. Microarthropods can also be extracted by shaking a soil sample in a dense salt solution. The organisms of interest float to the surface while the soil particles fall to the bottom of the container.

## Nematodes

Nematodes (Animalia, Nematoda: Adenophorea and Animalia: Nematoda: Secernetea), also known as roundworms, are cylindrical, unsegmented worms with tapered ends. They are small enough (100–1000  $\mu\text{m}$  in length and 5–100  $\mu\text{m}$  in diameter) to fit within the existing pore structure of soil, especially within soil aggregates. Like other soil microfauna, nematodes are aquatic organisms. Their habitat is the water films and water-filled pores with diameters similar to their body diameter.

The mouth and esophagus of nematodes show a wide variety of shapes that are generally related to their feeding habits. There appear to be two general strategies of feeding. One group has a **stylet** or a tooth to puncture living cells and suck out the cytoplasm, while the

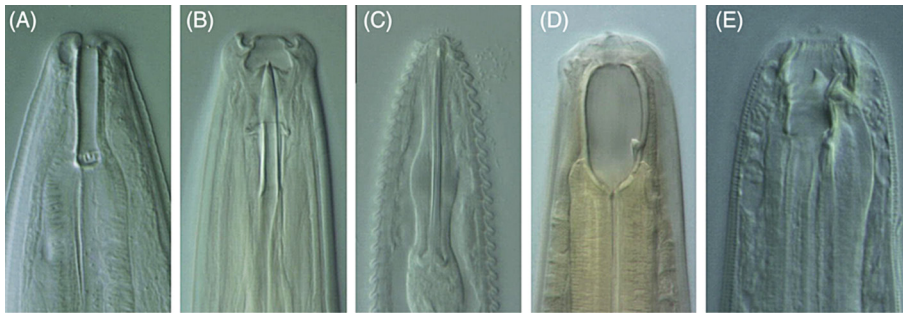


**FIGURE 8.8 Nematodes in different trophic groups are identified by the shape of their mouth and esophagus.** (A) *Rhabditoides inermis*, a bacteriovore, uses its stoma to feed on bacteria; the plant-feeding nematodes *Paractinolaimus* sp. (B) and *Mesocriconema* sp. (C) use a hollow stylet to puncture and feed on the contents of plant roots, as do nematodes that feed on fungi; predatory nematodes such as *Coomansus zschokkei* (D) and *Monochoides* sp. (E) use their large teeth to puncture their prey. Source: Adapted from Kiontke and Fitch (2013). Photo credit: (A, E) K. Kiontke, (B-D) De Ley Lab. Used with permission.

second ingests food whole. Nematodes can, as a first approximation, be classified into five major trophic groups (Yeates et al., 1993), depending on the morphology of the esophagus and mouthparts (Fig. 8.8):

- Bacteriovores are relatively small and have a **stoma**, an orifice that allows them to feed on bacteria.
- Predators use a very large stoma and tooth-like structure to prey on other nematodes.
- Fungivores use a slender stylet or a small tooth to puncture fungal hyphae and suck out the contents of the cell.
- Plant feeders puncture plant roots with a large stylet. Like fungivores, they feed on cytoplasm, sucking out the contents of the root cell.
- Omnivores are less specialized in their feeding habits, eating plant roots, protozoa, algae, fungi, and bacteria. Omnivores are sometimes combined with predators into a single category because many predaceous nematodes also appear to feed on other types of organisms.

A distinction is often made between free-living and **parasitic** nematodes. Free-living nematodes include bacteriovores, fungivores, predators, and omnivores, whereas parasitic nematodes are the plant feeders. Parasitic nematodes may live outside their hosts (ectoparasitic) or within them (endoparasitic) and can be free-living in their infectious, larval stage.

Nematodes are found in every ecosystem on earth. Their numbers range from less than  $10^6 \text{ m}^{-2}$  in desert soils to  $10^7 \text{ m}^{-2}$  in grasslands. Nematodes from all trophic groups are most abundant in surface soil horizons, with their numbers diminishing exponentially with depth. Within surface soils, free-living nematodes tend to be more numerous near patches of decomposing organic matter (e.g., plant litter, decaying insect remains), whereas plant feeders are most abundant in **rhizosphere** soil (Chapter 11). The rhizosphere and drilosphere are also regions of the soil containing high numbers of microbes. These in turn are resources for **microbivorous** nematodes and protozoa; therefore, populations of bacteriovores and fungivores are also more abundant in those habitats than in bulk soils.

Nematodes can be extracted from soil with a *Baermann funnel* (Fig. 8.7). The apparatus consists of a funnel fitted with a mesh to which a length of plastic tubing is attached. The tubing is clamped at the bottom and filled with water, the soil sample is placed on the mesh, and the funnel is filled with water to saturate the soil. Nematodes migrate out of the soil into the water-filled plastic tubing. Because they cannot swim effectively outside the narrow passages of soil voids, they collect at the clamped end of the tube. The clamp is then opened to collect the nematodes for enumeration and identification. Nematodes can also be extracted by wet sieving soil through successively finer mesh. The sieved soil is suspended in a concentrated sucrose solution and centrifuged. Because the specific gravity of nematodes is less than the concentrated sucrose solution, the nematodes float to the top while soil particles and other debris fall to the bottom of the centrifuge tube. This is known as the sugar flotation method.

## Protozoa

Soil protozoa (Protozoa: Ciliophoran, Discomitochondria, Rhizopoda) are unicellular organisms ranging in size from 6 to 100  $\mu\text{m}$  in diameter. Like nematodes, they are aquatic. They are sufficiently small to reside within the existing water-filled pores of soil aggregates. Many protozoa are **bacteriovorous**, but their diet may also include other protozoa, fungi, and organic detritus. Some ingest their food by engulfing it, whereas others brush food toward their mouth or **cytosome**. Protozoa are classified based on their morphology and means of locomotion:

- **Flagellates** (Fig. 8.9A). These protozoa rely on single or multiple **flagella**, long, whip-like appendages, for their motility. Flagellates feed primarily on bacteria and tend to be the most numerous of the soil protozoa.
- **Amoebae**. Amoebae extend and contract their protoplasm (the extensions are called **pseudopodia**) to move within soil pores. Two types of amoeba are recognized: *testate* and *naked*. Testate amoebae are encased in a rigid siliceous or chitin-based shell, or **test** (Fig. 8.9B), whereas the naked amoebae lack such a structure (Fig. 8.9C). Because of

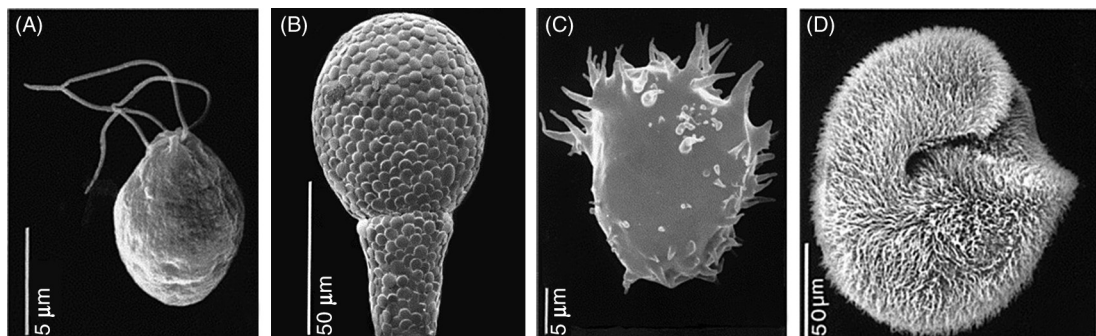


**FIGURE 8.9** Examples of soil protozoa. (A) *Polytomella* sp., a common heterotrophic soil flagellate. (B) *Nebela vas*, a testate amoeba. The shell is made of circular platelets originating from its prey, another testate amoeba, *Trinema lineare*. (C) *Mayorella* sp., a naked amoeba with cone-shaped pseudopodia mainly in the anterior body half. (D) *Bresslauides discoideus*, a large ciliate. Source: From Foissner (1999).

their ability to change shape, naked amoebae can explore smaller soil pores than testate amoebae, ciliates, or flagellates. Amoebae are common in the rhizosphere and at root surfaces, where they graze on the bacterial population.

- **Ciliates** (Fig. 8.9D). Ciliated protozoa move by beating the numerous **cilia** that cover the cell surface. Cilia are much shorter than flagella. Ciliates are well known for their ability to graze on bacteria, but about half of the known soil ciliate species prey on protozoa, including other ciliates.

Protozoa can make up a significant fraction of the faunal biomass in soil in agricultural ecosystems (Fig. 8.3). Their numbers range from  $10^9$  to  $10^{10}$   $\text{m}^{-2}$ , and they are more abundant in cultivated than in uncultivated soils. The most common way to enumerate protozoa is the **most probable number (MPN)** method, which involves serial dilution to the point where protozoa are no longer present (Box 8.4).

#### BOX 8.4

##### The most probable number (MPN) method of enumeration

Like the dilution plate count method (Fig. 5.8), the MPN method is a way to count organisms. It is the method of choice for enumerating protozoa in soil samples. To do an MPN assay, a series of increasingly dilute soil suspensions are prepared, to the point at which protozoa are no longer present (i.e., dilution to extinction). The dilutions are incubated with a growth substrate (e.g., bacteria) that allows the protozoa to reproduce. Samples are then examined microscopically for the presence of particular groups of protozoa. Replicate dilutions are inoculated into tubes or microplate wells in order to ensure accuracy. Positive replicates at particular dilutions are used to calculate the number of protozoa in the original soil sample using an MPN table or software program.

For example, assume that a number of 10-fold dilutions ( $10^{-2}$ ,  $10^{-3}$ ,  $10^{-4}$ ,  $10^{-5}$ ,  $10^{-6}$ , and  $10^{-7}$ ) are made of a sample, and each dilution is inoculated into four replicate wells of a 24-well microplate. After a suitable

incubation period, a sample from each well is examined, and the presence of protozoa is recorded (“+” = protozoa present; “-” = no protozoa). In this example, the number of positive replicates is 4-4-3-2-0-0 for dilutions of  $10^{-2}$ – $10^{-7}$ . Using these values to read the corresponding table indicates that the MPN is 21,000 individual protozoa  $\text{g}^{-1}$  in the original soil sample (Woomer, 1994).

The MPN method is also useful for enumerating many other microorganisms, such as cyanobacteria and algae that are challenging to grow on solid media.

|   |           |           |           |           |           |           |
|---|-----------|-----------|-----------|-----------|-----------|-----------|
| 1 | +         | +         | +         | +         | -         | -         |
| 2 | +         | +         | +         | -         | -         | -         |
| 3 | +         | +         | -         | +         | -         | -         |
| 4 | +         | +         | +         | -         | -         | -         |
|   | $10^{-2}$ | $10^{-3}$ | $10^{-4}$ | $10^{-5}$ | $10^{-6}$ | $10^{-7}$ |
|   | Dilution  |           |           |           |           |           |

## Fauna in the context of the soil food web

The activities of soil fauna take place in the context of the **soil food web** (Fig. 8.1). Because soil animals constitute only a small fraction of the biomass of heterotrophic soil organisms (Fig. 8.3), their importance in soil ecosystems results more from their ecological interactions with other microbes rather than their total biomass. These interactions mediate the transfer of carbon and nutrients, which originate in plant material, among **trophic groups** in the soil. Transfer of matter from one trophic level to the next becomes more inefficient as one moves up the trophic levels of the food web. One of the important consequences of such interactions is the release of nutrients through mineralization, especially phosphate and ammonium, from organic materials that form the detritus and the biomass of soil organisms. Plants require a source of inorganic (mineralized) nutrients, thus mineralization by the soil fauna contributes to plant productivity. This mineralization is particularly important for maintaining soil ecosystems, which are driven by the inputs of energy and nutrients entering the soil from plant residues.

The connectivity between trophic levels of the below-ground food web depends in part on the soil water dynamics. For aquatic fauna like nematodes and protozoa, accessibility of prey may become limited when soils dry. At the pore scale, plants can easily remove moisture from the relatively large pores of the nematode and protozoan habitat, thus reducing the spaces that can be explored for food by these aquatic animals. This will affect mineralization rates and plant nutrient availability.

Differences in soil habitat translate into differences in ability of fauna to interact with soil microorganisms within the soil foodweb. Members of the microfauna, many of which prey on bacteria, inhabit the same intraaggregate spaces that bacteria do but can be excluded from some of the bacterial habitat when soils dry. Fungal hyphae grow inside and outside aggregates, where **fungivorous** micro- and mesofauna can eat them. The macrofauna, on the other hand, interact with soil microorganisms at different levels, ranging from fortuitous ingestion to “engineering” their habitat to favor soil microorganisms that are part of their diet.

### Direct effects of the soil fauna on microbial communities

**Grazing.** The soil fauna and microflora form part of food webs in which they are both consumers and are themselves consumed (see Chapter 10). Soil food webs are driven by the chemical energy contained in detritus that is harnessed by soil microorganisms. Energy and nutrients are passed through the trophic levels of a food web. The consumption of microorganisms by the fauna is called grazing. Grazing accelerates the detrital microbial pathway of nutrient mineralization. There are three main aspects of grazing that affect functioning of the soil ecosystem:

- Reduced microbial biomass due to predation
- Changes in community composition
- Mineralization and release of nutrients from microbial biomass that is consumed

Grazers directly affect microbial biomass by removing individual microorganisms from the population. Yet predicting the effect of grazing on microbial populations is not as straightforward as it may appear. Intuitively, one expects the population size to decrease with grazing,

but grazing can also accelerate microbial growth rates (Bengtsson et al., 1993; Traunspurger et al., 1997). In fact, microbial population size may increase, decrease, or remain the same in response to grazing. What determines the outcome depends on factors such as the intensity of grazing, the initial size of microbial populations, and nutrient and energy limitations.

The accelerated growth rate that results when bacteria and fungi are grazed by collembolans, protozoa, and nematodes is called **compensatory growth**. Compensatory growth is a well-known effect in aboveground ecosystems. A familiar example is mowing a lawn periodically. Mowing removes some biomass and adds detritus, making a mown ecosystem more productive than one that is not. Similarly, in the grasslands of the Serengeti, grazing by zebras and antelopes stimulates plant growth.

**Nutrient cycling.** The soil fauna contributes considerably to nutrient cycling. Indeed, soil fauna may contribute as much as 30% of the total soil mineralizable nitrogen (Chapter 15). The contributions can be even higher in environments where microorganisms predominantly immobilize the nitrogen, particularly where detrital C/N ratios are high, and are partly a result of compensatory growth. The fauna remobilizes nutrients as metabolic waste products, which benefits both plant nutrition and microbial growth. Grazing results in net nutrient mineralization because feeding and digestive processes are never 100% efficient and C/N ratios of microorganisms and grazers differ.

In general, both the elemental compositions of grazers and microorganisms, and the physiological efficiencies of grazers, affect carbon and nutrient mineralization. Consider bacteria with a C/N ratio of 5 and bacteriovorous nematodes with a C/N ratio of 6. For every 6 units of bacterial biomass C consumed, nematodes receive 1.2 units of N. Nematodes only need 1 unit of N per 6 units of carbon. Thus, there is an excess of 0.2 units of N that may be excreted by the nematode as ammonia or readily mineralizable N compounds.

The discrepancy between C/N ratios of microbivorous animals and microorganisms is only half the mineralization story. Consider protozoa and bacteria, both with C/N ratios of 5. Protozoa, like all heterotrophs, meet their energy and carbon requirement by metabolizing organic carbon compounds and assimilate only a fraction of the carbon they consume into their biomass; the rest is lost as carbon dioxide. Assuming a C assimilation efficiency of 50%, protozoa would have to metabolize 10 units of C from the bacterial pool, corresponding to 2 units of N, to assimilate 5 units of C. This would leave 1 unit of N that cannot be used by the protozoa and may be mineralized. This example applies equally to microbivorous nematodes.

The effects of grazing on nutrient transformations also need to be placed in the context of soil physical constraints. There are two main hypotheses on the effect of changing soil moisture on grazing pressure by protozoa and nematodes. On the one hand, the *exclusion hypothesis* (Hassink et al., 1993) states that as soils dry and water films of soil particle become thinner, fewer of the most abundant types of aquatic grazers (nematodes and protozoa) can access their microbial prey and nutrient turnover decreases as a result. On the other hand, the *enclosure hypothesis* (Görres et al., 1999) states that as soils dry, aquatic grazers are concentrated in pockets of remaining soil water where they can consume microorganisms more readily, because they do not have to search for them as extensively. Because the coverage of soil particle surfaces with bacteria may be as low as 8% (Postma and van Veen, 1990) and searching for bacteria may be an important energy expenditure for the microbivorous fauna, “enclosure” would result in more rapid nutrient turnover, albeit in a smaller space. Both hypotheses are probably valid depending on the prevailing soil moisture content.

**Microbial community composition.** The feeding habits of soil fauna can affect not only the size but also the species composition of the microbial community. Microarthropods, free-living nematodes, and protozoa can be selective in their feeding, grazing preferentially on particular microorganisms. Selection may be based on size or other, often unidentified, characteristics of the microorganism. For example, some fungivorous nematodes and collembolans feed preferentially on plant pathogenic fungi. Furthermore, grazing can alter the outcome of competition for food resources between groups of microorganisms. For example, grazing of fungi by collembolans gives bacteria a competitive advantage. Not only do fewer fungi compete for food resources, but grazing additionally releases nutrients from fungal biomass for use by the resident bacterial community.

### Indirect effects of the soil fauna on microbial communities

**Primary production.** Grazing of soil microorganisms by soil fauna can have both negative and positive effects on primary production. On the one hand, plant parasitic nematodes are best known for their negative effects on crop production, which can potentially reduce the amount of plant detritus deposited on the soil surface. Because the soil food web is detrital, reduced litter inputs can decrease the numbers and activities of soil microorganisms. On the other hand, the mineralization of bacterial biomass by the soil fauna, as well as moderate levels of faunal feeding on plant roots, increases plant biomass production by increasing the size of the pool of above- and below-ground plant litter that fuels the soil food web. For example, small or moderate levels of root consumption by nematodes may enhance the growth rate of roots, an effect analogous to compensatory growth exhibited in grazed microbial populations and savannah grass. Injury to roots caused by root-feeding nematodes can result in additional carbon exudation from roots as well as root death, providing additional resources to fungi and bacteria.

As mentioned earlier, burrowing by earthworms alters the physical structure of soil, which in turn affects the availability of habitat and the movement of air and water in soil. Earthworms also impinge on the soil microbial community by translocating resources. Endogeic earthworms translocate and enrich the mineral soil they ingest by mixing it with intestinal secretions, enhancing microbial activity and nutrient turnover in the casts they produce. Similarly, anecic earthworms translocate large amounts of mineral soil from within the soil profile to the surface. They also drag plant litter into their burrows and line their burrows with mucus as well as nutrient-enriched castings. This enrichment generally increases microbial respiration and nitrogen mineralization, as well as numbers of autotrophic nitrifiers ([Chapter 15](#)). Conditions within the burrow can also promote the proliferation of fungi. Populations of microbivorous fauna, especially nematodes and protozoa, tend to be higher in the soil surrounding earthworm burrows than in soil without such burrows. Thus, the combined activities of earthworms, soil microorganisms, and the microbivorous fauna enhance decomposition of plant detritus and accelerate the release of nutrients in plant-available form.

**Transport.** In combination with their interaction with soil microorganisms, soil fauna of all sizes, including earthworms, microarthropods, nematodes, and protozoa can transport microorganisms through the soil profile. Transport can have positive effects for soil microbial populations, such as providing opportunities for the colonization of new habitat. Transport begins by soil animals ingesting cells and reproductive or survival structures, such as fungal

and bacterial spores. These structures are not always digested by soil animals and may instead be activated by passage through the gut. As soil animals move through the soil and excrete their wastes, they release bacteria and various types of spores away from where they were originally ingested. A second mechanism involves transport on the surface of soil animals, where spores and bacterial cells can attach themselves. As soil animals travel through the soil, microorganisms and their spores may become detached from their surfaces and deposited.

The ability of soil fauna to transport microorganisms has been used to inoculate large volumes of soil with bacteria for specific purposes. For example, earthworms can enhance the distribution of fungi and bacteria that are pathogens of insects, as well as bacteria that have been genetically engineered to enhance biodegradation of organic contaminants. However, not all microorganisms transported by the soil fauna have a positive effect on the soil. Soil animals can just as easily transport plant pathogenic fungi and their spores, and this transport may increase the likelihood of encountering a susceptible host plant.

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### Summary

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The soil fauna include earthworms, collembolans, mites, nematodes, and protozoa. These are eukaryotic, heterotrophic, motile organisms that require oxygen for their metabolism. Their physical range, habitat, and food resources are constrained by their respective sizes and the availability of pores of appropriate size within the soil. Nematodes and protozoa are microbivorous aquatic organisms, living within water-filled pores in aggregates and water films on particle surfaces, where they can access microbial and faunal prey. Collembola and mites are aerial organisms that live in interaggregate spaces or at the soil surface, feeding on fungi, plant detritus, microfauna, and other microarthropods. Earthworms are organisms that can live at the soil–litter interface or in burrows within the soil, feeding on soil or plant detritus. The interactions of the soil fauna with microorganisms take place in the context of the soil food web. Through grazing on bacteria and fungi, microbivorous faunal species directly affect the size and composition of microbial communities, populations of plant pathogenic microorganisms, and the mineralization of nutrients. They act to accelerate decomposition and nutrient cycling in soil. As a result of their feeding, burrowing, and movement, the soil fauna also engineer the habitat for the soil microflora, transport beneficial as well as pathogenic microorganisms, and affect the production of detrital resources from plants. The contribution of the soil fauna to the flow of nutrients and energy through soil ecosystems is disproportionately larger than their contribution to the total biomass of soil.

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### Study questions

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1. How would trophic interactions between soil fauna and microorganisms change as the soil water potential changes from saturated (0 MPa) to field capacity (−0.03 MPa) to permanent wilting point (−1.5 MPa)?
2. A nematicide is applied annually to an agricultural field. What may be the long-term consequences of this practice to (1) free-living nematodes, (2) microbial biomass, (3) N availability, and (4) the farmer's profits?

3. Farmer Ebe's fields are next to an old industrial site contaminated with 2,4,5-trichlorophenoxyacetic acid (2,4,5-T). The soil at the site is being bioremediated using anecic earthworms to distribute a genetically modified microorganism (GMO) within the soil profile. The GMO is a *Pseudomonas* species containing a plasmid that codes for the enzymes involved in the biodegradation of 2,4,5-T. Farmer Ebe is concerned that the activities going on at the neighboring bioremediation site are affecting his farm. He's noticed that the 2,4-dichlorophenoxyacetic acid (2,4-D) he has used for the past 20 years to control broadleaf weeds isn't working anymore. His raspberry plants have started to develop galls. He blames the bioremediation project for his problems and is considering suing the large conglomerate that owns the property. Develop scenarios that support Farmer Ebe's interpretation of the facts, as well as alternative scenarios.
4. As part of a demonstration project, a farmer has managed nutrient cycling in a tomato field by adding microbivorous nematodes annually (For examples of the successful use of nematodes in managing soil fertility, see Ferris, 1998). This year he has received a contaminated nematode culture that includes 5% predatory nematodes. Should he be concerned about this year's nutrient management success?
5. Septic system drainage fields remove pathogens from household sewage. One obvious mechanism involves mechanical removal by filtration, especially in conventional systems that drain in the C horizon. However, in novel systems, drainage is closer to the soil surface because treatment relies on the "biologically active zone" of the soil profile. What sorts of interactions might take place between microbial pathogens in the sewage and the soil fauna?
6. Climate change activists demand that all organic soils (northern forests, thawing permafrost in the Tundras) be inoculated with earthworms so the organic matter can be physically protected in earthworm castings. Argue for and against this idea.

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